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DOUGLAS-FIR BEETLE: A PROBLEM ANALYSIS

by

Norman E. Johnson^{1/}

The Douglas-fir beetle (Dendroctonus pseudotsugae Hopk.) presents a constant threat to the Douglas-fir forests of the Northwest. Sporadic attacks by this beetle probably have killed more Douglas-fir in Oregon and Washington than any other insect (126). In the wake of catastrophic high winds, fire, or drought, this insect builds up huge populations in windthrown, fire-killed, or weakened timber. Heavy winds of winters of 1949-51 downed more than 10 billion board feet of Douglas-fir timber in western Washington and Oregon (53). Beetles emerging from this timber killed an additional 3 billion board feet of green timber. Because of the threat from this outbreak, a Douglas-fir Beetle Committee was formed in the Northwest Pest Action Council (54).

^{1/} The author, Forest Entomologist at the Weyerhaeuser Forestry Research Center, expresses appreciation for review suggestions to the following forest entomologists: Malcolm M. Furniss of Inter-mountain Forest and Range Experiment Station, Kenneth H. Wright of Pacific Northwest Forest and Range Experiment Station, Dr. L. H. McMullen and M. D. Atkins of Forest Biology Laboratory in Victoria, Professor J. A. Rudinsky of Oregon State College, and Professor R. W. Stark of University of California. Thanks are extended also for technical editing, critical review and constructive revision at our Forestry Research Center by W. H. Cummings, Dr. E. C. Steinbrenner, and more particularly Leon F. Pettinger.

Outbreaks of the Douglas-fir beetle may be of profound importance to forest managers. Glascock (51) points out that the 1949-53 beetle outbreak caused a major shift of emphasis in logging plans in western Oregon. Lauterbach (79) recommended rapid expansion of road systems into areas of epidemic beetle infestation with aggressive salvage programs to reduce the beetle populations and to reduce timber losses caused by deterioration. His recommendation appears to have been a major influence in expansion of roads in the subject area of Douglas-fir beetle infestations. Smyth (121) reports that in 1951-52, sixty miles of logging roads were pushed into the forest on the heavily infested Millicoma Forest Tree Farm of Weyerhaeuser Company. The road construction crews were placed on double shift, and machinery fitted with lights to extend work to early morning and late evening hours. In order to handle the extra flow of logs produced on this crash program, the large mill at Coos Bay, Oregon, was placed on a two shift operating basis. Cornelius (31) emphasized how the beetle changed development plans, forced harvest in excess of allowable cut, and aggravated the fire hazard. Mahaffay (82) in a popular article featured the situation in Coos and Douglas Counties as a lesson of the need to maintain vigilance in the future.

The importance of the Douglas-fir beetle warrants appraisal of the need for expanded research effort. The present paper has been prepared to facilitate such appraisal. Specific objectives are (1) to review current available literature on the Douglas-fir beetle, (2) to identify aspects apparently deserving further study, and (3) to outline contemplated research on the Douglas-fir beetle at the Weyerhaeuser Forestry Research Center.

Description, occurrence, morphology

Dr. A. D. Hopkins first published a description of the Douglas-fir beetle in 1901, followed by several significant reports through 1915 (55, 56, 57, 58, 59). These include details on description and keys on external morphology for larvae, pupae, and adults. Dendroctonus pseudotsugae and D. simplex are distinguished from other species by the character of epistoma, and from each other by the sculpture of the pronotum and difference in size. Swaine (23) gives this concise description of the adult Douglas-fir beetle:

"Length, 3.5 mm to 7 mm, average nearly 6 mm; dark brown to nearly black with the elytra often red; the epistomal process with the sides parallel and with its anterior margin usually projecting slightly beyond the margin of the epistoma; the pronotum shining, finely, closely punctured, with a few larger punctures intermixed."

The use of immature stages in the family Scolytidae for taxonomic purposes has met with considerable difficulty. Thus the families Scolytidae and Curculionidae had not been separated on the basis of larval characteristics (18, 104). Thomas (124) working with 30 species of bark beetles -- D. pseudotsugae not being included -- has been able to make critical distinctions both between and within genera.

The distribution map (58) shows the beetle occurring throughout the range of Douglas-fir: in the Pacific Coast region from British Columbia to California, in the Rocky Mountain region from Canada to Mexico.

Hosts of the Douglas-fir beetle listed by Chamberlin (24) include western larch and bigcone Douglas-fir (Pseudotsuga macrocarpa) in addition to Douglas-fir. Attacks by this beetle occur on western redcedar when near Douglas-fir logs. Attacks have also been reported in Brewer spruce (Picea breweriana)^{2/}, and in western hemlock, with broods produced in some instances.

Chamberlin (23) features the external morphology of Dendroctonus in abbreviated form; Swaine (123) illustrates external morphology of Scolytidae using Hylurgops as a model. On the internal anatomy of the Douglas-fir beetle the nervous system has been worked out and the male and female reproductive system illustrated (5). A technique for measuring reported anatomical changes in flight muscles has been described (7). Ryan (115) showed that during diapause the wing muscles of the Douglas-fir beetle were reduced and no eggs were present in the ovaries and the seminal vesicles were underdeveloped in the male. The developmental stages of the beetle -- egg, larva, pupa, adult, and also ovaries are diagrammed (127). Studies on the mountain pine beetle dealing with internal changes associated with egg-laying (107) and morphology (108) should prove of help in interpreting the morphology of the Douglas-fir beetle. External indications of the sex of Dendroctonus beetles are slight. Hopkins (58) used a number of diverse characteristics, which as pointed out by Lyon (80) do not occur universally throughout the genus. This results in the necessity of using a combination of several characters for accurate sexing. He then pointed out that the presence or absence of the stridulating organ, a process of the seventh abdominal tergite, is a flawless indicator of sex in Dendroctonus beetles. The stridulating organ occurs in the male. Chapman (28) used the sounds produced by the stridulating organ for sex determination. Vaughan McCowan^{3/} found that the elytral declivity of the female was distinctively rougher to touch than that of the male.

^{2/} Observations by Kenneth H. Wright, Pacific Northwest Forest and Range Experiment Station.

^{3/} Former Entomologist, Weyerhaeuser Company.

Nutrition, physiology, activity

On nutritional studies with the Douglas-fir beetle very little has been reported. Chapman (26) observed beetles to feed on several types of moist paper and a number of vegetable foods as well as apple and coconut meat. In no case was the rate of feeding on these strange substances as great as on normal Douglas-fir bark. Nutritional studies (29) were conducted on treated paper made from a dissolving grade of western hemlock pulp. These papers impregnated with glucose, mannose, galactose, ribose, arabinose, starch and pectin, showed that beetles did not distinguish between these carbohydrates. At Corvallis, Oregon, Douglas-fir beetles were fed a solution of 2.5 percent glucose containing 2.5 microcuries of P^{32} per milliliter (39). After the radioactive phosphorus was incorporated into the body, the beetles were macerated and analyses run. Radioactive phosphorus was found in the head, thorax, abdomen, legs and wings. The wings contained a greater amount than reported for other insects in similar studies. Some radioactive phosphorus was found in phospholipids, but 93 percent was recovered in difference phosphorylated intermediates -- 3-phosphoglycerate had the highest concentration.

In a recent physiological study in Oregon (111) the Douglas-fir beetle shows positive phototaxis between 9°C and 34°C . Below and above this range the response was generally reversed. When the beetles are placed in a temperature gradient in the absence of light, they avoided temperatures above 32°C and preferred temperatures around 21° and 22°C . Hopping (61) reports the negative geotaxis of female beetles in constructing galleries in standing trees, or logs that are not lying level. However, the beetle will nearly always construct its gallery parallel to the grain of the tree. Thus the gallery will be above the entrance hole except in logs that are lying level. Atkins (9) used a flow of air along with a source of light to direct Douglas-fir beetles into a position for photography. This indicated a positive response to light and air currents; however, Atkins (3) had indications that flight was usually down-wind.

A recent study on limits of activity (111) for the Douglas-fir beetle has identified the lower limit as between 0°C and 1°C . At 1°C slow leg movement begins; at 2°C the beetle is able to stand but unable to move forward. Restrained movement takes place at $3-4^{\circ}\text{C}$. Beetles kept for several days at 7°C recovered when exposed to $+22^{\circ}\text{C}$. Temperatures higher than $33-36^{\circ}\text{C}$ result in excessive activity. Beyond $38-39^{\circ}\text{C}$, at low relative humidity heat injury resulted. The thermal death zone was reported at between 47° and 49°C , where independent of relative humidity death occurs in 1 to 3 minutes. At relative humidity of 40 percent, temperatures of $40-42^{\circ}\text{C}$ proved lethal to beetles in a few hours, whereas at relative humidity of 100 percent they could withstand the same temperatures for several days. Further lab-

oratory studies (111) on running showed that maximum locomotion without flight took place at around 29° C where the beetles averaged 70-80 cm/min. At temperatures between 33° and 46° C excessive activity occurred with the beetles showing symptoms of erratic wandering and stumbling. Below 4° C the beetle is not capable of regulated running. The effect of solar radiation was also demonstrated. Beetles placed in the sun at air temperatures of 9° C and 25° C reacted at rates comparable to those in the shade at 16-17° C and 40-45° C, respectively. At 25° C air temperature in direct sunlight beetles began to succumb -- this occurs at 45° C without solar radiation.

Chapman (25) in laboratory flight studies found that Douglas-fir beetles attached to a flight mill could fly continually up to 9 hours at velocities of 35 to 40 meters per minute. Previous history of the adults was important in determining whether or not flight would take place. Beetles emerging from logs of their own accord flew better than those taken during gallery construction. Within the zone of general flight ability, temperature had little direct influence on flight capacity (111). In the absence of sunlight, wings were spread only rarely below 18° C. Between 18° C and 20° C no flight was attempted in absence of sunlight. At 22° C many beetles engaged in flight whereas at around 25° C flight attempts are the rule. From 25-32° C the beetles are able to continue in flight after colliding with an object. The influence of solar radiation was such that in the sunlight even at an air temperature of 21° C flight was near maximum. Atkins (10) showed that changes occurred in the flight muscles of females soon after gallery construction began. Degeneration of flight muscle tissue seems to be correlated with maturation of the ovaries and laying of eggs. In some beetles no flight muscle degeneration took place and thus these beetles could leave the original host and make a second attack. No regeneration of flight muscles has been reported. In an experiment with light, Atkins (10) showed that at an intensity of 0.5 foot candles or lower, no flight took place and the percent of flight response increased up to 35 foot candles. Atkins presented evidence that the presence of mites and nematodes had no effect on response to flight. Free flight velocity ranges from around 50 to 150 meters per minute or about three times the velocity measured on flight mills (6, 111). The wing beat frequency was shown to be slightly influenced by temperature once the beetles start flying. At 11° C the beats averaged 71 per second; at 15° C 80; at 20° C 88, and at 31° C 90 beats per second. Atkins (6) demonstrated an increase of wing beat frequency with a lowering of atmospheric pressure. Atkins (11) has reported that high relative humidity increases the possibility of spontaneous flight at sub-optimal temperatures and decreases it at high temperature. He also reported on frequency and amplitude of wing beat, flight duration, and velocity as related to light, temperature, atmospheric pressure, and associated organisms. Of all of the flight movements, wing beat frequency was most affected by environmental factors.

Tests of effect of temperature on boring activity of female beetles (111) indicated the maximum amount of frass was removed from the gallery at a temperature of 32° C. Detectable changes in boring activity were noted with daily temperature changes. Ryan (115) in a study on rearing the Douglas-fir beetle found that if the beetles were allowed to develop under a constant temperature, emergence of adults was delayed and took place over a period of several months. He then subjected beetle infested logs to 75° F for periods of 40, 80, and 120 days. Following this, logs were placed at temperatures of 33, 39, 43, 49 and 55° F for periods of 20, 50, and 90 days. After analysis and plotting the data, the optimum temperature for diapause development was found to be 44° F. The minimum development period at 75° F was between 40 and 80 days. The minimum duration of cold treatment that was effective was between 20 and 50 days.

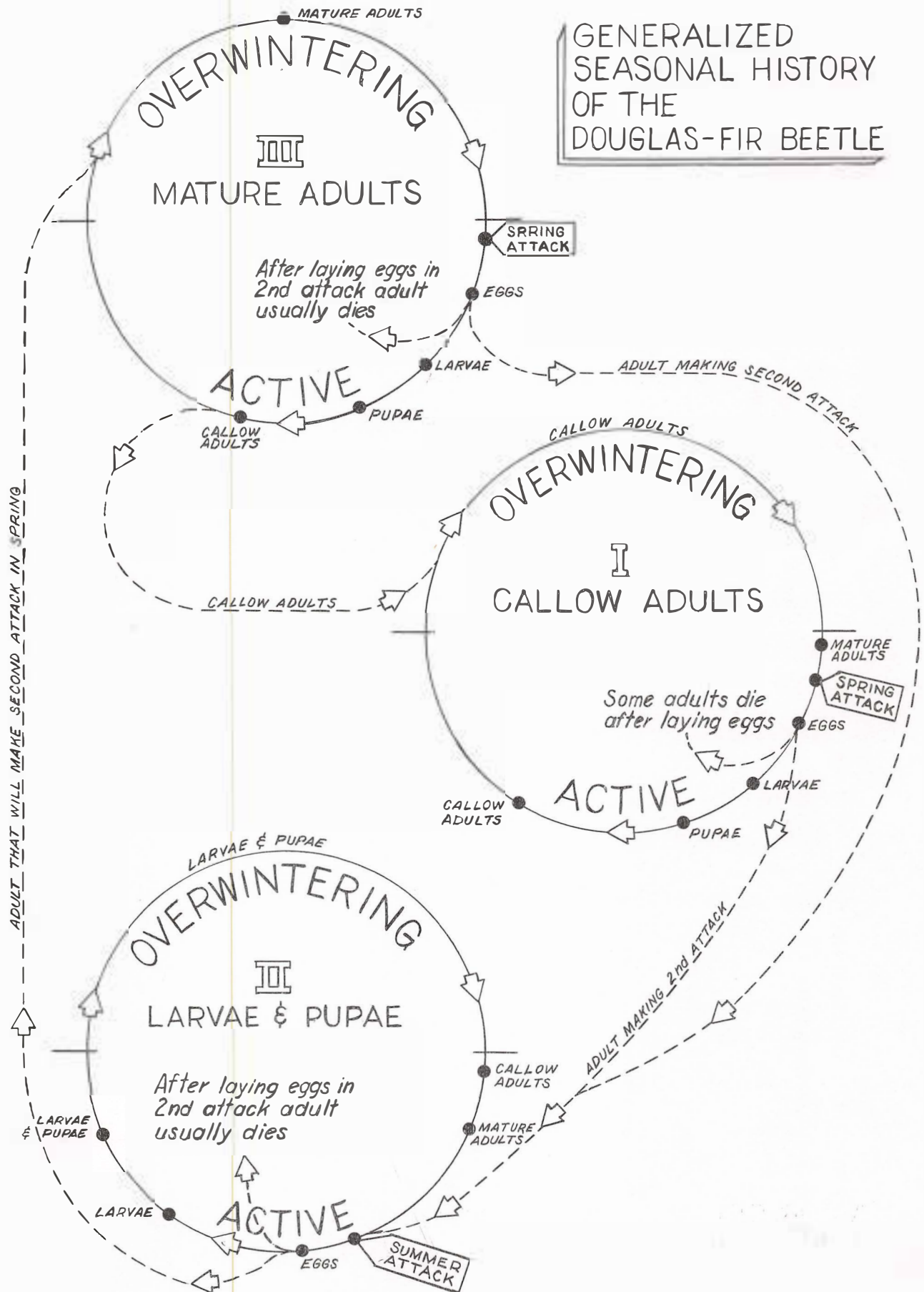
Seasonal history and brood development

The seasonal history of the Douglas-fir beetle as with other insects depends a great deal on the climatic conditions during the spring and summer months. Figure 1 presents a summary diagram based on observations by a number of workers (17, 22, 38, 41, 57, 58, 85, 87, 133). The Douglas-fir beetle has a one year life-cycle with two broods per generation. There is considerable overlap in the emergence and attack periods of the two broods. The beetles overwinter mostly as callow adults (I, Figure 1), but a number of larvae and pupae are also found (II, Figure 1). Overwintering callow adults mature and emerge in the spring to attack fresh logs and green trees, whereas the overwintering larvae mature to adults during the spring months and make summer attacks. The overwintering adults consist mainly of the completed brood of beetles making a spring attack. However some adults that make their initial attack in the summer months may overwinter to make a second attack in the spring (III, Figure 1). The overwintering larvae are the broods of the beetles making their second attack in the summer. The spring attack is recorded as occurring from the middle of April to mid-July in western Oregon; the summer attack from July 26 to mid-September (85). Others report the spring attack from April to early June and the summer attack in July and August (38). Walters (133) states that in the interior of British Columbia the spring attack occurs from late April to mid-June and the summer attacks about six weeks later. Hopkins (57) and Chamberlin (22) indicate that some of the more advanced brood may start a second generation. In work carried out near Cowichan Lake, British Columbia, it was found that the peak of attacks occur in May with another slight peak in early July (30). McMullen and Atkins⁴ found in their experiments that 50 percent of the females made a second attack with some females constructing 3 or 4 galleries.

⁴/ Personal communication from Dr. L. H. McMullen, Victoria, B. C., April 1960.

FIG. 1

GENERALIZED
SEASONAL HISTORY
OF THE
DOUGLAS-FIR BEETLE



Prepared by L.F. PETTINGER
DEC. 1960

Drawn by F.G.M.

Upon finding a suitable host, the female bores into the bark and starts constructing an egg gallery in the phloem. The gallery is constructed parallel to the grain and usually upward. Chamberlin (22) reports that mating takes place in the galleries, but does not describe the process. Reid's (106) description of the mating of the mountain pine beetle may be similar but remains to be checked. After constructing about an inch of gallery the female begins to deposit eggs. The female usually constructs egg grooves from $\frac{1}{2}$ to several inches long on alternate sides of the egg gallery. However, in the presence of abnormal bark conditions or the presence of other phloem miners, the egg grooves will vary. Within these grooves egg niches are made and one to several eggs are deposited. Galleries in which the female is successful in laying eggs vary from one inch to over three feet in length. The average length of egg gallery varies according to observer and region: 8 to 10 inches in British Columbia (133); from 5-12 inches in our Northwestern states (38). The number of eggs laid varies considerably, from about 50 to occasionally 300 (127, 133). Over a three year period, the number of eggs per inch of gallery in logs near Coos Bay, Oregon, averaged a little greater than 10 (85). It was reported that the relationship between the length of parent gallery and the number of eggs per lineal inch of gallery may be an index to reproductive potential. Here, the parent galleries constructed in down logs in 1953 were $\frac{1}{2}$ to $\frac{2}{3}$ shorter than those in 1952, a period in which the beetle populations were declining. In the Rocky Mountain region, Furniss (42) found about 8 eggs per lineal inch of gallery constructed. In current research Dr. L. H. McMullen reports⁴ a correlation between the number of eggs per inch of gallery and the attack density.

The duration of the egg stage varies considerably. Chamberlin (22) found the incubation of the eggs took 15 to 21 days. Others give 7 to 10 days (13, 38). Under laboratory conditions at 21.5° C the incubation period averaged 6 days (127); 5 stages of development in the egg were recognized on basis of the enclosed embryo. The newly hatched larvae is about 1.5 mm long with a pointed abdomen and a non-tanned head capsule that is 0.55 mm wide. Although five instars have been reported (14) it is accepted that there are only four (87, 111, 145).

The larval stadia lengths were given as 4, 5, 6, and 15 days for the 1st, 2nd, 3rd, and 4th instars, respectively (111). This was at 21.5° C. At this same temperature, the pupa underwent 4 externally recognizable changes which took 10 days before the adult stage was reached. At Trinity Field Station in British Columbia the larval stadia were reported as lasting 6, 15, 15, and 19 days. The overall period of development from egg to callow adult has been reported as: 91 days (13); from 62 to 120 by other authors in the field and as short as 33 days in the laboratory at 29-30° C (127). At 11-12° C the development was estimated to be at least

150 days. All field observations apparently refer to the spring broods, without mention of the development of the progeny of the summer broods. Some indication has been given (87) that the development of overwintering larvae, at least in the laboratory occurs at an accelerated rate in the spring, resulting in additional overlapping of the flight periods.

Freshly emerged callow adults do not possess mature sex organs, but sexual maturity is gained after 2-3 weeks at 22° C, (127). The sex ratio is 1:1 (13) if taken from the brood before emergence from the galleries. However in the field the females are usually more numerous. Possible reasons given for this change in sex ratio are: (1) the females can complete a second attack without being refertilized; (2) the male is more exposed to predaceous insects, and (3) the males are faced with a greater task of finding first a suitable host which may or may not contain female beetles. In their search they may be lost by their wide-spreading, excessive activity or to predaceous insects (127). In experiments in which the number of male and female beetles were controlled, it has been shown that a ratio of 3 males to 4 females would allow complete fertilization (127).

Mortality considerations

Both low and high temperatures are reported to cause brood mortality in the Douglas-fir beetle. McMullen (86) noted abnormal mortality of Douglas-fir beetle broods following the sudden cold spell in November 1955. Cold weather in May 1953, following a short warm period was suspected as being one of the decisive factors in reducing Douglas-fir beetle population (85). With the western pine beetle, Miller (93) found that all overwintering larvae were killed when bark temperatures reached -10° F and all adults at 0° F. When air temperatures drop to -37° F to -44° F a large proportion of overwintering *D. brevicornis* are killed (69). Beal (12) demonstrated that with an air temperature of -26° F, the subcortical temperature of ponderosa pine logs with bark $\frac{1}{2}$ inch thick was -17° F, and only 0° F in logs with bark $1 \frac{3}{4}$ inches thick. Mortality of broods of the western pine beetle was 73 percent in the thin-barked trees and 34 percent in the thick-barked trees.

High temperatures also have a profound effect on brood development and survival. Trees in logging settings, windthrown trees, and road right-of-way logs which are exposed to direct sunlight show high brood mortality (85). Douglas-fir beetles in thin-barked trees exposed to the direct rays of the sun have three times the mortality measured in the fall of the year, than those in thick-barked logs in the shade (65). Miller (93) in studies with the western pine beetle found that complete mortality occurred when subcortical temperatures reached 120° F. He also demonstrated that bark temperatures in the direct rays of the

sun may be as much as 40° F higher than air temperature. In thin-barked trees, this method has been effective in control of the mountain pine beetle (102).

The relation of other climatic factors to mortality in the Douglas-fir beetle have not been measured. Chamberlin (23) cites evidence that heavy rains, wind, and drought may be important factors affecting the beetles directly or through their influence on predators, parasites or disease. Furniss (42) found that slabs of infested Douglas-fir that were coated with paraffin had greater emergence of beetle than unparaffined slabs. This indicates a relationship between survival and moisture content.

An important source of mortality is the overcrowding by adjacent broods. It has been found that where successful attacks numbered more than 8 per square foot, overcrowding and competition for food would cause larval mortality (85). However a lesser number of attacks may result in mortality from intra-specific competition. Canadian entomologists^{2/} indicated that in their area 4 to 6 attacks per square foot is considered optimum for brood production.

A great number of predaceous and predatory insects, mites, nematodes, centipedes, fungi, yeasts and bacteria have been found associated with the Douglas-fir beetle. Chamberlin (23) gives an excellent review of the early literature. Bedard (16) has published an impressive list of the predators, parasites and associated insects of the Douglas-fir beetle. Furniss (41, 42, 43, 44) has studied many natural control factors, many reported for the first time. Bedard (13) felt that Thanasimus dubius Fab. was the most important predator of the Douglas-fir beetle in eastern Washington. Furniss (41) gives evidence that this species may actually be Thanasimus undatulus Say. Enoclerus sphegeus and Medetera aldrichii are reported to be the more important predators in western Oregon (85). Hopping (62) feels that M. aldrichii is more effective than any other predator with the possible exception of Enoclerus sphegeus. Hopping (62) and DeLeon (33) have studied the biology of M. aldrichii. Furniss (42) feels that the predatory ability of the ostomid, Temnochila virescens is greater than supposed by other authors. Struble (122) and Reid (105) have reported on the biology of Enoclerus sphegeus with the former including studies of Temnochila virescens. (See Table 1)

Chamberlin (23) reports three species of mites that are known predators of eggs and early stages of Douglas-fir beetle. The known predators are: Pediculoides ventricosus, Seius safoi, and Parasitus sp. Bdella magna is possibly predaceous. Rust (144) reports 62.5 percent egg mortality caused mostly by Parasitus sp. In Canada, 33 percent reduction of broods was

^{5/} Conference with R. Lejeune, in Victoria, B. C. July 31, 1959.

Table 1. Parasitic and predaceous insects reported on the Douglas-fir beetle.

Family	Genus species	Reference
<u>Parasites</u>		
Braconidae	Cpelooides brunneri Vier.	13. 16. 42.
	C. dendroctoni Cush.	16.
	C. scolyti Cush.	16.
	Cecidostiba burkei Cwld.	23.
	C. dendroctoni Ashm.	16. 17.
Pteromalidae	Roptrocercus (Pachycercus) sp.	23.
	R. (P.) eccoptogastri	17.
	Tomicobia tibialis Ashm.	46.
	Theocolaxia (Cercocephala) Colon (L)	16.
<u>Predators</u>		
Staphylinidae	Quedius marginalis	16.
Histeridae	Isolomalus mancus Casey	16.
Cucujidae	Cucujus clavipes Mann.	23.
Nitidulidae	Pityophagus rufipennis Horn	23.
Ostomidae	Temnochila virescens Mann.	23. 42.
Cleridae	Enoclerus sphegeus Fabr.	16. 23. 42.
	E. lecontei Wolc.	16. (85. 105.)
	Thanasimus dubius (Fab.)	16. 44.
	(= T. undulatus)	
Tenebrionidae	Hypophloeus substriatus	16.
Cicindelidae	Cicindela longilabris	22.
Dolichopodidae	Medetera aldrichii Wh.	16. 32. 42.
	M. oregonensis V. Duz.)	(62. 85.)
	M. sp.)	46.
Lonchaeidae	Lonchaea corticis Taylor	15.
Asilidae	Desyllis pasticata	22.
Anthocoridae	Ardus debilis Uhler	16.
	A. proboscideus Walker	16.

found in beetles infested with mites (133). The mites infesting the beetles in this study were: Calvolia sp., Dendrolaelaps quadrisetis, Lasioseius sp., Parasitus sp. and Uropoda sp. Furniss (42) has found a number of additional species of mites, many of which have only been identified to family. Those identified to genus include: Ensliniella, Gamasellus, and Histiostoma. The predatory nature of these mites was not determined. Atkins (10) found that infestation of Douglas-fir beetles by mites did not affect the beetles' natural flight response. The mites incurred were: Dendrolaelaps sp., Vidia sp. and Uropoda sp. He also reports a Vidia species as occurring internally.

Chamberlin (23) reports that Fuchs in 1914 found nematodes associated with bark beetles and at that time stated that they weaken the beetles and may reduce egg laying up to 40 percent. Workers in British Columbia (85) have found Aphelenchulus sp. and Aphelenchulus reversus in the body cavity; Aphelenchoides near talonus under elytra; Aphelenchoides latus, Rhabditis obtusa, and Panagrodontus near dentatus in the frass. Tests conducted with nematodes of the genera Aphelenchulus spp. and Cheilobus spp. (85) found that Aphelenchulus spp. had a greater effect on vigor and fecundity than did Cheilobus spp. Khan (71, 72, 73) has described three species of nematodes, Sphaerularia (now Stictylus (74)) ungulacaudus, S. hastata, and Ektaphelenchus macrostylus from the Douglas-fir beetle. Furniss (44) reports Aphelenchulus reversus, Diplogaster sp., Parasitaphelenchus sp., Rhabditis obtusa, and Ektaphelenchus obtusus as being found associated with the Douglas-fir beetle in Idaho. Atkins (10) found parasitic nematodes of the genus Sphaerularia in addition to those found by other authors. He also found Diplogaster stercorarius associated with the beetle.

Various investigators (42, 85) have sent what appeared to be diseased Douglas-fir beetle larvae to specialists, but in all instances no known pathogenic bacteria or viruses were found. Yeasts have been recorded of the genera Hansenula, Candida, and Saccharomyces in association with the Douglas-fir beetle (81). A recent article (21) summarizes available information on the yeasts associated with bark beetles. Bedard (17) reports that the Douglas-fir beetle carries spores of Ceratocystis minor (Hedgc.) Hunt. (Ceratostomella pseudotsugae) with them into the trees and thus spread the fungus. In Coos County, Oregon, this blue stain fungi was often present in the galleries of the Douglas-fir beetle (85). It was thought at that time that if the fungus developed and spread faster than the larvae were able to mine, it would cause mortality of the beetles by reducing the nutritive value of the inner phloem.

Host relationships

Hopkins (57) recognized the association of Douglas-fir beetle outbreaks with drought and with excessive quantities of felled or windthrown trees. Bedard (17) contends that logging slash, fire-scorched and windthrown trees provide the preferred type of host material for the Douglas-fir beetle. Furniss (47, 48, 49) points out that the Douglas-fir beetle is a common killer of living trees around the periphery of recently burned over areas. He reports that following the great Tillamook fire of 1933, 200 million feet of green timber was killed by the Douglas-fir beetle. It has been shown that the amount of tree killing by the Douglas-fir beetle increased markedly one year following heavy blowdown (146). In the interior of British Columbia it is believed that tree killing is primarily associated with logging operations (128, 133). It has been pointed out that timber felled in the course of road construction also provides the beetle with an excellent opportunity to maintain high population levels (85).

It is generally accepted that bark beetle epidemics are closely allied with weather conditions. Doane, et al (34) and Bedard (17) indicate that the Douglas-fir beetle is more aggressive in the more arid portions of its range and once outbreaks develop they subside more slowly than in the moist forests of the coast. Wright (144) believes that the great bark beetle epidemic of 1950-53 in Oregon and Washington was associated with drought conditions of 1951 and 1952 as well as with the windthrow. Walters (131) found heavy mortality due to Douglas-fir beetle in trees suffering from winter injury in British Columbia.

Trees weakened by defoliation are especially susceptible to attack by the Douglas-fir beetle (38). Heavy tree killing by the Douglas-fir beetle has been reported following defoliation by the hemlock looper and spruce budworm (109, 138). There is some indication that trees with root rot (Poria weirii) may be more susceptible to bark beetle attacks (146). At least the increased windthrow in root rot-infested stands contribute to increasing beetle populations. However, trees with butt rot are apparently no more heavily attacked than healthy trees (101).

The susceptibility of standing green Douglas-fir to bark beetles has been studied much less than the susceptibility of pines. Walters (129) reported a tree classification for Douglas-fir based on risk of attack by the Douglas-fir beetle. The workability of this system is not reported in literature. Mathers (84) found no correlation of attack of the Douglas-fir beetle with crown size, shape of the trunk or diameter at breast height. However, he did show a significant correlation of attack with growth rate in the outer $\frac{1}{2}$ inch. The slower growing trees had the greatest attack. Injured trees regardless of growth rate were more susceptible to attack. In other

reports (85, 125) beetle-attacked trees when compared to the nearest unattacked tree had significantly slower growth for the preceding 25 year period. It has been suggested (64) that low vigor trees are most susceptible to attack by the Douglas-fir beetle under endemic conditions, but that high vigor trees may be susceptible in epidemics. Walters (133) and Furniss (45) report that trees over 150 years in age appear to become susceptible to attack. Wright (143) has correlated the lack of vigor of Douglas-fir trees in western Oregon with moisture deficiency and has found indications that bark beetles may be more successful in attacking trees of low vigor. Suppressed trees have been reported as commonly attacked but rarely producing broods (99).

Little work is reported concerning what actually attracts Douglas-fir beetles to its host, nor has it been established whether the beetle flies at random or is guided by olfactory sense. However, several exploratory studies of interest may give some clues to this mystery. Kinghorn (78) states that the Douglas-fir beetle will attack trees within hours after felling. In his study he cut 16 inch blocks from Douglas-fir trees. One group of blocks was immersed in water, another was left at room temperature in polyethylene bags, a third at room temperature without polyethylene, and a fourth left in the woods. After three weeks the treated blocks were returned to the field where they were exposed to attack along with those left in the woods. None of the blocks were attacked by the Douglas-fir beetle, whereas the remainder of the tree from which the blocks were cut was heavily attacked. On the other hand, the short blocks were attacked more heavily than the remaining tree boles by the ambrosia beetle, Trypodendron lineatum, an insect that has been shown to prefer trees felled several months prior to attack. Kinghorn's conclusion was that the xylem and phloem cells of the short logs went through a more rapid change or decomposition. Sections of Douglas-fir logs standing on end sustain significantly fewer attacks than those lying on the ground (8). The bark surface on down logs is exposed to more direct solar radiation than that on standing sections. This could affect the attraction of beetles through rate of drying out or release of volatile substances. Johnson (67) examined over 200 living Douglas-fir having beetle attacks, and found that the proximity to fresh windthrow or felled trees influenced the proportion of trees attacked.

On both standing and windthrown trees at Coos Bay, Oregon, the number of attacks per square foot increased from the base to the top until that point where the bark thickness became less than 0.3 inches (85). The basal 10-20 foot of standing trees was nearly devoid of attacks. Furniss (42) found that the lower 9 feet of standing trees generally had fewer attacks and they were quite erratic. On windthrown trees, Furniss (41) found the greatest difference in number of attacks around the circumference of the bole with fewest attacks on the top and exposed side. On well-shaded logs nearly twice as many attacks per square foot

were found as compared to those logs exposed to the direct rays of the sun (65). In southern Oregon, logging slash was not heavily attacked and only the larger logs produced broods which were concentrated on the underside (101).

Survey and sampling

Detailed surveys have been made on Douglas-fir beetle infestations in the Pacific Northwest since 1951, and for a longer period in British Columbia. Table 2 presents a conspectus of the trend in Douglas-fir beetle infestation over the past 9 years. It should be remembered that the mortality detected by aerial survey is the result of the previous year's attacks. Most of the trees killed in 1951 did not fade until the spring of 1952 (99). Aerial surveys have greatly facilitated the forest manager's problems in road building to remove windthrow and beetle-killed timber. Techniques, operation, and accomplishments of a detailed survey connected with the beetle epidemic of 1950-54 have been described (53). Colored aerial photographs have been useful in evaluating mortality of Douglas-fir and planning salvage operations (135, 136). A manual on forest insect survey and control methods has been compiled by Rudinsky (113).

Ground sampling methods most used are to remove a given area of bark and to count the number of attacks and brood survival. In studies at Coos Bay, Oregon (85), sampling units of 1, 2, and 4 square feet of bark area were taken at 10-foot intervals along the bole. The 1-square-foot unit was selected as the standard. Walters (130) used a 2-foot wide bark strip taken around the log at 10-foot intervals. Furniss (41) uses a 6" x 12" unit since it was found that the attack intensity was on the average much greater in the Rocky Mountain area as compared to the Pacific Northwest. He also used what he termed quadrant samples on down trees which were 12 inches long and equal in width to $\frac{1}{4}$ the circumference of the log. He took detailed information on each bark sample in indicated units: (1) Dimensions, $\frac{1}{2}$ -inch; (2) Diameter of trunk, 1/10-inch; (3) Bark thickness, $\frac{1}{4}$ -inch; (4) Attacks by Douglas-fir beetle, successful and unsuccessful, number; (5) Length of each beetle gallery, $\frac{1}{2}$ -inch; (6) Sex of parent beetles living and dead, number; (7) Brood stage of live and dead beetles exposed and hidden in bark, number; (8) Identity of all visible natural control organisms or associated insects, number; (9) Ventilation holes, number, and (10) Exit holes, number.

In measuring brood success Furniss (44) used the following formula:

$$\text{Survival percent} = \frac{\text{Number of live brood on sample}}{\text{Parent galleries, (inches) X 7.93 eggs/inch}} \times 100$$

Table 2. Summary of 1951-59 Douglas-fir beetle survey reports.

Year	Washington-Oregon, extent of infestation	British Columbia regions
1951	168,000 A. Beetles attacked, as expected, trees wind-thrown in 1949-50 and living trees. (95)	Coast, no reports of appreciable damage; inland, small groups throughout range of Douglas-fir. (35)
1952	4,570,130 A. Due to 1949-50 windthrow and 1951 droughts. (96)	Coast, first heavy mortality in years; inland, increased--no predicted decrease in 1953. (36)
1953	4,832,800 A. Some decline in west-side infestations. (97)	Coast, most severe infestation to date; inland, continued about as in 1952. (37)
1954	5,071,750 acres - Ground checks indicate attacks in 1954 are down, epidemic appears over. (98)	Coast, and inland, Douglas-fir beetle continued relentless destruction throughout Province. (116)
1955	873,120 A. Reduction in beetle populations in next few years is predicted. (138)	Coast, attacks no heavier in 1954; inland, continued killing, some evidence of decrease. (117)
1956	116,900 A. Continued decline in populations. (139)	Coast and inland, decline in beetle population, but heavy losses due to winter freeze. (118)
1957	18,400 A. Lowest damage in recent years; increase predicted due to windthrow of winter 1955-56. (140)	Coast and inland, generally low infestation, winter-damaged stands showed higher mortality. (119)
1958	880,160 A. Resulted from beetle populations built up in 1955-56 windthrow. (20)	Coast, reduced; inland, increase. (120)
1959	324,840 A. Most of damage east of mountains. (19)	

In a recent study in western Washington (65) the same formula was used, substituting 10 eggs per inch. In this study a 3.2 foot long sample strip was taken from around the stem at the butt, mid, and top 16-foot log of the tree. The center point of the sample was chosen from a table of random numbers and could fall anywhere along the 16-foot log except at the extremities. The 3.2 foot wide strip represents approximately 20 percent of the bark area of the log.

Special techniques

Several techniques have been developed for trapping, rearing, and following activity within the galleries. These will be helpful in further studies on the Douglas-fir beetles. Bedard (14) reared broods of Douglas-fir beetles in phloem strips pressed between two plates of glass held together by rubber bands. In one study (88) outer and inner bark was ground up in a household blender. Some of the ground-up bark was mixed with agar and water with sodium benzoate and Dowicide "A" added to part of the mixture. The best results were obtained when excess water was squeezed out and when sodium benzoate was added. Warren (134) used both a bark homogenate and whole bark pieces surrounded by moist cotton and pressed between glass plates to successfully rear weevil larvae. Reid (106) used a similar method with the mountain pine beetle, but sealed the glass with friction tape. Larvae were successfully transferred from one log to another by boring a small hole with an increment borer into the log to be infested, inserting a larva and sealing it over with grafting wax (88). On thin-barked logs a small chisel was used instead of the increment borer. X-ray has been successfully used to follow gallery construction and brood development in waxed rearing slabs that were used in laboratory rearing (66). A technique for following Douglas-fir beetle activity under bark has been devised at Corvallis, Oregon. The sounds of boring, stridulation, and other activities were tape recorded (1). A tent-cage constructed of nylon mesh was successful in caging fresh Douglas-fir logs for studies of Douglas-fir beetle attack and development (89).

Artificial control

Review of literature indicates the lack of a sound basis for silvicultural control of the Douglas-fir beetle. However any method of cutting that would minimize windthrow is to be recommended. The logging of injured, defoliated, fire-scorched, root-rot infected or slow growing trees will reduce damage. In the inland regions, both Walters (133) and Furniss (45) suggest that trees over 150 years old are a risk. Walters points out that over-mature, decadent stands often suffer considerable annual depletion and timber owners should give such stands priority in the cutting program. Infested windthrow material should be removed from the

woods as soon as possible and prior to beetle flight the following spring (63). Hopping (60) gives the following recommendations: (1) Log as soon as possible all areas showing bark beetle attack; (2) Place fresh slab, cull logs, tops, contiguous to old cuttings; (3) Burn slash at least once a year; (4) Avoid leaving logs in the woods longer than necessary in the spring; (5) Cut right-of-way as short a time in advance as possible; and, (6) Maintain a careful watch on timber surrounding logged areas and infested trees in case of shut-down of logging.

Furniss (45) emphasizes the importance of removing infested material before the stage that bark will fall off during logging. After one year it is almost impossible to skid an infested log without losing the bark and all the beetles it contains. Removal of logs to the mills and log ponds will reduce the number of beetles that will be available to attack the following year. However, Keen (70) states that the portion of the log that is floating out of the water will allow the broods to emerge. Both Walters (133) and Furniss (45) recommend having a supply of felled trees in the vicinity of windthrow or logs to absorb attacks -- these would then be removed from the woods during the summer. Hopkins (58) reports that trap trees should be felled in August and April. Those felled in August should be removed before winter and those felled in April before July. Walters (133) further cautions against injuring trees by fire, skidding or bulldozers since damaged trees are reported to be susceptible to attack.

In certain cases, one can resort to the methods of peeling and burning or piling and burning which are well covered by Keen (70) for pine bark beetles. Under certain conditions burning is a recommended method of control (17, 38, 133). Walters (133) also suggests that beetles can be destroyed by peeling the bark to expose the insects to sunlight. However, Patterson (102) and Miller (93) found that control by this method should not be attempted for western pine beetle and mountain pine beetle unless air temperatures of 80° F are reached.

Kinghorn (76, 77) treated infested Douglas-fir logs with formulations of ethylene dibromide, heptachlor, aldrin, and lindane. He reports that all insecticides were formulated at the rate of 3.2 pounds per 5 gallons except for lindane which was at 0.64 pounds. Heptachlor and aldrin were emulsifiable concentrates; ethylene dibromide and lindane were technical grade. Solvents were fuel oil for ethylene dibromide, acetone for lindane and water for the others. Ethylene dibromide, aldrin and heptachlor were effective against the Douglas-fir beetle in thin-barked trees. Concentrated schradan and systox was tested in frills in Douglas-fir trees in the hopes of making them into poison trap logs. Counts after the trees were felled and exposed to attack showed no difference between the insecticide-treated logs and unpoisoned controls, nor was the brood survival significantly different except right above the girdles.

Gibson (50) found that orthodichlorobenzene, trichlorobenzene, dichloroethylether and ethylene dibromide in either diesel oil or emulsion form gave good control of broods. He used one gallon of formulation for each 31 square feet of bark surface. Dry logs were more successfully treated than were those whose bark was wet or still had fresh phloem. Walters (133) reports on pilot tests in British Columbia that were successful in destroying broods of the Douglas-fir beetle. In these tests 15 pounds of ethylene dibromide and $2\frac{1}{2}$ pounds of emulsifier with enough fuel oil to make 4 Imperial gallons was added to 16 gallons of water. Application was made from a tank-type pressure sprayer. All the above chemical treatments were applied after the logs had been attacked. Benzene hexachloride, when applied to freshly felled Douglas-fir logs for the prevention of ambrosia beetle attacks, also reduced the number of attacks by the Douglas-fir beetle (75). Both a 2.5 and 5.0 percent oil emulsion of DDT made by diluting a 25 percent emulsifiable concentrate reduced the number of Douglas-fir beetles attacking fresh logs (85). Lindane, thiodan and sevin have been found to give protection up to 8 weeks, with sevin being the least effective and thiodan the most effective (2). Treated logs also had much less blue stain and sapwood-rotting fungi than untreated checks. The insecticides were 25 percent wettable powder for the thiodan and lindane and 50 percent wettable powder for sevin used at 1 and 3 pounds per hundred gallons of water. It was also noted that the gallery length was shorter and percent of successful brood was less on the treated than on the controls. At Oregon State College, entomologists (112) tested the following insecticides which are listed in decreasing order of effectiveness in killing the Douglas-fir by topical applicator: Lindane, thiodan, isodrin, endrin, sevin, heptachlor, aldrin, dieldrin, DDT, and chlordane. Endrin, thiodan and isodrin were characterized by long residual toxicity while lindane, aldrin, heptachlor and chlordane had a rapid decrease of toxicity in the first two weeks. DDT had the longest residual, but next to the lowest rate of kill.

Discussion of proposed studies

One important phase of the life-cycle of the Douglas-fir beetle concerns the second attack, or what would better be referred to as summer attack. The quantitative relationship of the number of beetles making a summer attack compared to the spring attack is not known. Opinion differs on the significance of the second or summer attack. Some workers feel that the second attack may cause nearly as much mortality as the first attack (85). In British Columbia it is felt that because the summer attack is less intense and more protracted than the spring attack, it is less critical in respect to infestation of living trees in the Inland Empire of British Columbia (87). Furniss (41) apparently feels the same regarding the summer attack in the Rocky Mountains. There are several reasons to believe that the summer attacks may

be of more significance than indicated. It has been reported that in many instances the second or summer attack is more successful because the intensity of attack is less, thus giving the developing broods more room and food (85). Martinek (83) found that with Ips typographus the second brood was characterized by longer galleries and greater survival.

Douglas-fir beetles are able to bore into trees at a faster rate at higher temperatures, (111) -- as during warmer summer months. It is postulated that this rate of boring may be related to the beetle's success in overcoming resistance of standing trees. Trees whose water supply is deficient have been shown to be more susceptible to attack by Ips typographus and Pityogenes chalcographus (90). This may be a decisive factor in the characteristically dry summer months of the Pacific Northwest forests. Merker (92) reports that trees with high osmotic pressures that usually occur in hot, dry weather are more attractive to bark beetles, mainly due to the stronger scent from the more concentrated cell sap. Knowledge of the quantitative aspects of the summer attack and the relative susceptibility of trees to attack during this period has immediate practical applications in scheduling logging of freshly felled timber and possible trap logs.

Pertinent to the logging of infested logs is fate of the beetles that fall to the forest floor and remain in pieces of bark that fall from the logs. As noted by Furniss (45), logs infested with the Douglas-fir beetle for several months lose their bark readily when being skidded. If a large proportion of the beetles that fall from the logs during logging remain alive over winter it would be beneficial to schedule logging prior to the time that the bark begins to slip from the logs.

Probably the greatest need for study concerns the various factors affecting the relation between the beetle and its host, the Douglas-fir tree. To our knowledge it has not been established whether the Douglas-fir beetle flies at random or whether it can seek out a suitable host from a number of unsuitable ones. With some scolytids there is a distinct guiding sense -- probably olfactory. The ambrosia beetle, Trypodendron lineatum, shows no trial-and-error settling on and sampling of unsuitable host material, but rather is guided by an olfactory sense by airborne odors emitted by the host (52). It was demonstrated that certain materials extracted in nitrogen at low temperatures were attractive to ambrosia beetles. Research in British Columbia⁵ indicates that attractiveness of a log may depend on whether female beetles are already present. Logs artificially infested with female beetles were attacked with greater density than uninfested logs or those in which only males were present. A number of workers, notably in Europe, have tested substances extracted from trees for their attractiveness to bark beetles. Merker (91) showed that Ips typographus had a stronger attraction for sap from its natural host, spruce, than for pine, silver fir, larch, Douglas-fir or western hemlock: The attractiveness was

due to some factor other than the sugar content of the phloem sap. Ohnesorge (94) reports that ether-soluble extracts of conifer bark and phloem contained substances attractive to the weevil, Hylobius abietis. However, the methyl ester of linolenic acid provided a stronger attractive force for this species than did spruce sap from its preferred host (68). In addition to attractive substances, certain authors have reported that toxic and repellent substances may occur in conifers. Perthunen (103) found that except at the very lowest concentrations alpha pinene was repellent to the bark beetle Hylastes aster. Other workers found that both alpha and beta pinene were not attractive to the ambrosia beetle Trypodendron lineatum and may have even shown a slight repellent action (137).

Other aspects of insect-host relationships needing attention concern such stand attributes as age, site quality, density, vigor, and the presence or absence of root rot. By knowing what constitutes a susceptible tree can one plan a silvical method of reducing damage to stands. As we approach a second-growth economy, investigations should be made to determine the brood productivity in young trees removed during weeding and thinning. We should also study factors that may lead to bark beetle losses in young stands competing for space to grow. As has been suggested earlier, the root rot Poria weirii may predispose trees to a attack (146). In Europe, Wichmann (141) found Fomes annosus directly associated with attacks by Dendroctonus micans. Francke-Grossman (40) reports that Armillaria mellea is more frequently than supposed the forerunner of attacks by bark beetles.

There is a real need for a complete analysis of the Douglas-fir beetle problem throughout its range. It is hoped that this review of literature will serve as a starting point for such an analysis. This will require the combined efforts of all those working with this important forest insect pest.

The Appendix includes an outline of things to be learned about any species of bark beetle. This outline was prepared by J. M. Swaine. After each topic in which work has been reported on the Douglas-fir beetle, references are listed. Those topics without references either have been studied and not reported or need study. The following list of suggested studies includes those planned for the Weyerhaeuser Forestry Research Center:

1. To perfect the method we have proposed of using a radioactive tag to follow the progress of the parent beetles under the bark and to be able to detect their emergence without destroying the brood. (Preliminary tests with existing equipment indicate that the position of a beetle can be located to the nearest $\frac{1}{2}$ inch).

2. To incorporate the radio-tracer technique into a study designed: (1) to measure the quantitative relationships between the spring and summer broods; (2) to test factors such as time of attack, density of attack, deterioration of food material, degree of shading, and moisture content of the phloem to see how they influence the second attack. This research is to be conducted under Professor R. W. Stark, University of California, by the author for partial fulfillment of the degree of Doctor of Philosophy.
3. To determine if the Douglas-fir beetle attacks its preferred host by alighting upon it in a random fashion or is guided by olfactory sense.
4. To see if forced attacks of Douglas-fir made at various times throughout the summer have varied success. Concurrently watering experiments will artificially manipulate the environment. A portable freezing unit will be employed to lower the temperature around the root collar of a tree thus reducing the water content.
5. To determine whether bark stripped from logs in the process of logging infested material will produce beetles for flight in the spring.

LITERATURE CITED

1. Allen, Donald G., R. R. Michael, and S. A. Stone. 1958. Sounds of Douglas-fir beetle activity. Ore. Forest Lands Research Cent. Research Note 36. 19 pp.
2. Allen, Donald G. and J. A. Rudinsky. 1959. Effectiveness of Thiodan, Sevin, and Lindane on insects attacking freshly cut Douglas-fir logs. Jour. Econ. Ent. 52: 482-484.
3. Atkins, M. D. 1957. Flight studies on the Douglas-fir beetle, Dendroctonus pseudotsugae Hopk. Canada Dept. Agr. Forest Biol. Lab., Victoria. Interim Rpt. 1956-2. 21 pp.
4. Atkins, M. D. 1957. A study of the effect of nematodes and mites on Douglas-fir beetle flight. Canada Dept. Agr. Bi-Mo. Progr. Rpt. 13(5): 2-3.
5. Atkins, M. D. and J. A. Chapman. 1957. Studies on the nervous system anatomy of the Douglas-fir beetle, Dendroctonus pseudotsugae Hopk. Scolytidae. Can. Ent. 89: 80-86.
6. Atkins, M. D. 1958. Further studies on the flight of the Douglas-fir beetle, Dendroctonus pseudotsugae Hopk. Canada Dept. Agr. Forest Biol. Lab., Victoria. Interim Rpt. 1958-3. 10 pp.
7. Atkins, M. D. and S. H. Farris. 1958. A technique for measuring flight muscle changes in the Douglas-fir beetle, Dendroctonus pseudotsugae. Canada Dept. Agr. Bi-Mo. Progr. Rpt. 14(4): 3-4.
8. Atkins, M. D. and L. H. McMullen. 1958. Selection of host material by the Douglas-fir beetle (Dendroctonus pseudotsugae). Canada Dept. Agr. Bi-Mo. Progr. Rpt. 14(1): 3.
9. Atkins, M. D. 1959. A method for the close-up photography of insect behavior. Can. Ent. 91: 328-29.
10. Atkins, M. D. 1959. A study of the flight of the Douglas-fir beetle (Dendroctonus pseudotsugae). I. Flight preparation and response. Can. Ent. 91: 283-291.
11. Atkins, M. D. 1960. A study on the flight of the Douglas-fir beetle, Dendroctonus pseudotsugae Hopk. Canada Dept. Agr. Forest Biol. Lab., Victoria. Interim Rpt. 1959. 66 pp.
12. Beal, J. A. 1934. Relation of air and bark temperatures of infested ponderosa pine during subzero weather. Jour. Econ. Ent. 27: 1132-1139, illus.

13. Bedard, W. D. 1933. The Douglas-fir beetle -- its seasonal history, biology, habits and control. U. S. Div. Forest Insect Field Sta., Coeur d'Alene, Idaho. Office Rpt. 67 pp.
14. Bedard, W. D. 1933. The number of larval instars of Dendroctonus pseudotsugae Hopk., with a method for their determination in relation to other bark beetles. Jour. Econ. Ent. 26: 1128-1134.
15. Bedard, W. D. 1937. Biology and control of the Douglas-fir beetle, Dendroctonus pseudotsugae. Wash. State Coll. Resid. Stud. 5: 103-105.
16. Bedard, W. D. 1938. An annotated list of the insect fauna of Douglas fir (Pseudotsugae mucronata Rafinesque) in the Northern Rocky Mountain Region. Can. Ent. 70: 188-197.
17. Bedard, W. D. 1950. The Douglas-fir beetle. U. S. Dept. Agr. Circ. 817. 10 pp.
18. Böving, A. G. and F. C. Craighead. 1931. An illustrated synopsis of the principal larval forms of the order Coleoptera. Ent. Amer. (n.s.) 11: 1-351.
19. Buckhorn, W. J. and P. W. Orr. 1958. Forest insect conditions in the Pacific Northwest during 1958. Pac. Northwest Forest and Range Exp. Sta. p. 14-16.
20. Buckhorn, W. J. and P. W. Orr. 1959. Forest insect conditions in the Pacific Northwest during 1959. Pac. Northwest Forest and Range Exp. Sta. p. 12-14.
21. Callaham, Robert Z. and Moshe Shifrine. 1960. The yeasts associated with bark beetles. Forest Sci. 6: 146-154.
22. Chamberlin, W. J. 1918. Bark beetles infesting the Douglas fir. Ore. Agr. Exp. Sta. Bul. 147. 40 pp., illus.
23. Chamberlin, W. J. 1939. The bark and timber beetles of North America. Ore. State Coll. Coop. Assn., Corvallis, Ore. 513 pp.
24. Chamberlin, W. J. 1958. The Scolytoidea of the Northwest. Ore. State Coll. Press, Corvallis, Ore. 205 pp.
25. Chapman, J. A. 1954. Flight of Dendroctonus pseudotsugae in the laboratory. Canada Dept. Agr. B1-Mo. Progr. Rpt. 10(4): 3.

26. Chapman, J. A. 1955. Ingestion of paper and vegetables by the Douglas-fir beetle, Dendroctonus pseudotsugae Hopk. Canada Dept. Agr. Bi-Mo. Progr. Rpt. 11(2): 3.
27. Chapman, J. A. 1955. Physiological and biological studies on the ambrosia beetle, Trypodendron lineatum (Oliv.) and the Douglas-fir beetle, Dendroctonus pseudotsugae Hopk. Canada Dept. Agr. Forest Biol. Lab., Victoria. Interim Rpt. 1954-2. 30 pp.
28. Chapman, J. A. 1955. Sex determination by stridulation sounds in the Douglas-fir beetle, Dendroctonus pseudotsugae. Canada Dept. Agr. Bi-Mo. Progr. Rpt. 11(3): 4.
29. Chapman, J. A. and J. W. Wilson. 1956. The use of impregnated paper as an approach to nutritional studies with the Douglas-fir beetle. Jour. Econ. Ent. 49: 426-27.
30. Chapman, J. A. and J. M. Kinghorn. 1958. Studies of flight and attack activity of the ambrosia beetle, Trypodendron lineatum (Oliv.) and other scolytids. Can. Ent. 90: 362-372.
31. Cornelius, Royce. 1955. How forest pests upset management plans in the Douglas-fir region. Jour. Forestry. 53: 711-712.
32. DeLeon, D. 1934. An annotated list of the parasites, predators, etc., of the mountain pine beetle. Can. Ent. 66: 51-61.
33. DeLeon, D. 1935. A study of Medetera aldrichii, a predator of the mountain pine beetle. Ent. Amer. 15: 60-90.
34. Doane, R. W., E. C. Van Dyke, W. J. Chamberlin, and H. E. Burke. 1936. Forest insects. McGraw-Hill Book Co., New York. 463 pp.
35. Evans, D., E. D. A. Dyer, D. A. Ross, and P. A. Jones. 1951. Province of British Columbia. In Annual Report of Forest Insect and Disease Survey. Canada Dept. Agr. Forest Biol. Div. p. 108, 110.
36. Evans, D., E. D. A. Dyer, D. A. Ross, and P. A. Jones. 1952. Province of British Columbia. In Annual Report of Forest Insect and Disease Survey. Canada Dept. Agr. Forest Biol. Div. p. 130, 133.
37. Evans, D., G. T. Silver, and D. A. Ross. 1953. Province of British Columbia. In Annual Report of Forest Insect and Disease Survey. Canada Dept. Agr. Forest Biol. Div. p. 139, 142.

38. Evenden, J. C. and K. H. Wright. 1955. Douglas-fir beetle. U. S. Dept. Agr. Forest Pest Lft. 5. 4 pp.
39. Fang, S. C. and Donald Allen. 1955. Radioactive phosphorus in the Douglas-fir beetle. Jour. Econ. Ent. 48: 79-82.
40. Francke-Grosmann, H. 1954. Populationdynamische Faktoren bei der Massenvermehrung des Dendroctonus micans Kug. an der Sitkafichte in Schleswig-Holstein. Verhandlungen der deutschen Gessellschaft für angewandte. Entomologie, Verlag P. Parey, Berlin. pp. 108-117.
41. Furniss, Malcolm M. 1956. Study plan for investigations of the Douglas-fir beetle, Dendroctonus pseudotsugae Hopk., in the Intermountain region. Intermountain Forest and Range Exp. Sta. 10 pp.
42. Furniss, Malcolm M. 1957. Investigations of the Douglas-fir beetle, Dendroctonus pseudotsugae Hopk., in the Intermountain region. Intermountain Forest and Range Exp. Sta. Progr. Rpt. 1956. 60 pp.
43. Furniss, Malcolm M. 1957. Investigations of the Douglas-fir beetle, Dendroctonus pseudotsugae Hopk., in the Intermountain region. Intermountain Forest and Range Exp. Sta. Progr. Rpt. 1957. 51 pp.
44. Furniss, Malcolm M. 1958. Investigations of the Douglas-fir beetle, Dendroctonus pseudotsugae Hopk., in the Intermountain region. Intermountain Forest and Range Exp. Sta. Progr. Rpt. 1958. 26 pp.
45. Furniss, Malcolm M. 1959. Reducing Douglas-fir beetle damage -- how it can be done. Intermountain Forest and Range Exp. Sta. Research Note 70. 6 pp.
46. Furniss, Malcolm M. 1960. Douglas-fir beetle research in the Intermountain area -- A problem analysis. Intermountain Forest and Range Exp. Sta. 54 pp. In manuscript.
47. Furniss, R. L. 1936. Bark beetle activity following Tillamook fire. Timberman 37(3): 21-22.
48. Furniss, R. L. 1937. Salvage on Tillamook burn as affected by insect activity. Lumberman 39(2): 11-12.
49. Furniss, R. L. 1941. Fire and insects in the Douglas-fir region. Ore. State Forester Circ. 3.

50. Gibson, Archie L. 1957. Tests of bark-penetrating insecticides to control the Douglas-fir beetle. Jour. Econ. Ent. 50: 266-269.
51. Glascock, H. R., Jr. 1953. Beating the beetle in the Douglas fir region. Western Forestry Conf. Ann. Proc. 44: 45-46.
52. Graham, K. and A. E. Werner. 1956. Chemical aspects of log-selection by ambrosia beetles. Canada Dept. Agr. Bi-Mo. Progr. Rpt. 212(1): 3-4.
53. Greeley, A. W., K. H. Wright, and R. B. Pope. 1953. Final report on the 1952 blowdown -- bark beetle survey in the Douglas-fir region of Oregon and Washington. Pac. Northwest Forest and Range Exp. Sta. 14 pp.
54. Hagenstein, W. D. and R. L. Furniss. 1955. Cooperation speeds salvage of windthrown and beetle-killed timber in Oregon and Washington. Soc. Amer. Foresters Mtg. Proc. p. 167-168.
55. Hopkins, A. D. 1901. Some insect enemies of living trees. Soc. Promotion Agr. Sci. 22nd Ann. Mtg. Proc. (Denver, Colo.): 66-69.
56. Hopkins, A. D. 1903. Forest insect explorations in the summer of 1902. Can. Ent. 35(3): 59-61.
57. Hopkins, A. D. 1909. Practical information on the Scolytid beetles of North American forests. I. Barkbeetles of the genus Dendroctonus. U. S. Dept. Agr. Bur. Ent. Bul. 83, Part 1. 169 pp.
58. Hopkins, A. D. 1909. Contributions toward a monograph of the Scolytid beetles. I. The genus Dendroctonus. U. S. Dept. Agr. Bur. Ent. Tech. Ser. 17: 1-164.
59. Hopkins, A. D. 1915. Contributions toward a monograph of the Scolytid beetles, II. Preliminary classification of the superfamily Scolytoidea. U. S. Dept. Agr. Bur. Ent. Tech. Ser. 17: 165-232.
60. Hopping, George R. 1932. Control of Douglas-fir bark beetles. Timberman 33(7): 61.
61. Hopping, G. R. 1942. Apparent negative geotropism in the Douglas-fir bark beetle. Can. Ent. 74: 205.
62. Hopping, George R. 1947. Notes on the seasonal development of Medetera aldrichii Wheeler, as a predator of the Douglas-fir bark beetle, Dendroctonus pseudotsugae Hopkins. Can. Ent. 79: 150-153.

63. Hopping, Ralph. 1921. The control of bark beetle outbreaks in British Columbia. Canada Dept. Agr. Circ. 15 pp.
64. Intermountain Forest and Range Experiment Station. 1958. Highlights in research -- Annual Report. p. 23.
65. Johnson, Norman E., P. W. Orr, and K. H. Wright. 1959. Beetle hazard in windthrown Douglas-fir. Weyerhaeuser Research Note 20. 3 pp.
66. Johnson, Norman E., and H. David Molatore. 1960. X-ray detection of Douglas-fir beetles reared in slabs. Can. Ent. In press.
67. Johnson, Norman E. and Leon F. Pettinger. 1960. Douglas-fir beetle attacks in living trees as influenced by the presence of fresh windthrow. 6 pp. In manuscript.
68. Kauth, H. and W. Madel. 1955. "Über die Ergebnisse der im Schwarzwald and Hunsrück von 1952-1954 durchgeführten Freilandversuche zur anlockung des grossen braunen Fichten rüsselkäfer, Hylobius abietis L. mit Lockstoffen Z. Angew. Ent. 37: 245-9.
69. Keen, F. P. and R. L. Furniss. 1937. Effect of subzero temperature on population of western pine beetle, Dendroctonus brevicornis. Jour. Econ. Ent. 30: 482.
70. Keen, F. P. 1952. Insect enemies of western forests (rev.). U. S. Dept. Agr. Misc. Publ. 273. 280 pp., illus.
71. Khan, M. A. 1957. Sphaerularia bombi Duf. (Nematoda: Allantonematidae) infesting bumble bees and Sphaerularia hastata n. sp. infesting bark beetles in Canada. Can. Jour. Zool. 35: 519-523.
72. Khan, M. A. 1957. Sphaerularia unguilacauda sp. nou. (Nematoda: Allantonematidae) from the Douglas-fir beetle, Dendroctonus pseudotsugae Hopk., with key to Sphaerularia species. Can. Jour. Zool. 35: 635-639.
73. Khan, M. A. 1960. Descriptions of two nematodes, Ektaphelenchus macrostylus n. sp., and Laimaphelenchus ulmi n. sp., with a key to species of Laimaphelenchus. Can. Jour. Zool. 38: 91-97.

74. Khan, M. A. 1960. Styctylus hastatus (Khan, 1957) n. comb., and Styctylus unguilacaudus (Khan, 1957) n. comb. (Nematoda: Neotylenchidae). Can. Jour. Zool. 38: 225-226.
75. Kinghorn, J. M. and W. E. Webb. 1950. Chemical control of ambrosia beetles. Canada Dept. Agr. Bi-Mo. Progr. Rpt. 6(6): 2-3.
76. Kinghorn, J. M. 1953. Chemical control of bark beetles. Canada Dept. Agr. Bi-Mo. Progr. Rpt. 9(4): 3.
77. Kinghorn, J. M. 1955. Chemical control of the mountain pine beetle and Douglas-fir beetle. Jour. Econ. Ent. 48: 501-504.
78. Kinghorn, J. M. 1957. An induced differential bark-beetle attack. Canada Dept. Agr. Bi-Mo. Progr. Rpt. 13(2): 3-4.
79. Lauterbach, Paul G. 1952. Douglas-fir beetle situation on Weyerhaeuser Timber Co. ownership in Oregon. Weyerhaeuser Timber Co. 41 pp. Processed.
80. Lyon, R. L. 1958. A useful secondary sex character in Dendroctonus bark beetles. Can. Ent. 90: 582-584.
81. Lu, K. C., Donald G. Allen, and Walter B. Bollen. 1957. Association of yeasts with the Douglas-fir beetle. Forest Sci. 3: 336-343.
82. Mahaffay, Robert E. 1948. The killer. Amer. Forests 54(2): 64-65, 80.
83. Martinek, V. 1956. An attempt at explaining the problem of sister broods in I. typographus. Sborn. čsl. Adad. zeměd. (Lesn.) 29: 615-44.
84. Mathers, W. G. 1951. Douglas-fir beetle. Canada Dept. Agr. Bi-Mo. Progr. Rpt. 7(3): 3.
85. McCowan, Vaughan F. and Julius A. Rudinsky. 1958. Biological studies on the Douglas-fir bark beetle, Millicoma Forest Tree Farm, Coos Bay, Oregon (revision of '54 issue). Weyerhaeuser Forestry Research Note 11. 21 pp.
86. McMullen, L. H. 1956. A note on mortality of the Douglas-fir beetle in the interior of British Columbia during the winter of 1955-56. Canada Dept. Agr. Bi-Mo. Progr. Rpt. 12(6): 3.

87. McMullen, L. H. and J. Walters. 1956. Bionomics of the Douglas-fir beetle, Dendroctonus pseudotsugae Hopk., in the interior of British Columbia. Canada Dept. Agr. Forest Biol. Lab., Vernon, B. C. Interim Rpt. 1955-2. 25 pp.
88. McMullen, L. H. and J. Walters. 1956. Transplanting the larvae of Dendroctonus pseudotsugae Hopk. Canada Dept. Agr. Bi-Mo. Progr. Rpt. 12(3): 3.
89. McMullen, L. H. and M. D. Atkins. 1959. A portable tent cage for entomological field studies. Ent. Soc. B. C. Proc. 56(4): 67-68.
90. Merker, E. and H. Muller. 1951. Die Abhängigkeit des Frasses der Fichtenborkenkäfer vom Bodenklima. Allg. Forst-u. Jagdztg. 123(1): 16-20.
91. Merker, E. 1953. Lockstoffe und Nährstoffe in Wirtspflanzen einiger Waldschädlinge. Allg. Forst-u. Jagdztg. 124(5): 138-44.
92. Merker, E. 1956. Der Widerstand von Fichten gegen Borkenkäferfrass. Allg. Forst-u. Jagdztg. 127(7; 8/9): 129-45; 168-87.
93. Miller, J. M. 1931. High and low lethal temperatures for the western pine beetle. Jour. Agr. Research 43: 303-321.
94. Ohnesorge, B. 1953. Der Einfluss von Geruchs und Geschmacksstoffen auf die Wahl der Frasspflanzen beim grossen braunen Rüssel-Käfer Hylobius abietis L. Beitrage zur Entomologie 3(5): 437-68.
95. Oregon State Board of Forestry and U. S. Bur. Ent. and Plant Quar. 1951. Report of forest insect detection surveys in Oregon and Washington. (Nov.) p. 23.
96. Oregon State Board of Forestry and U. S. Bur. Ent. and Plant Quar. 1952. Report of forest insect surveys in Oregon and Washington. (Nov.) p. 23.
97. Oregon State Board of Forestry and U. S. Bur. Ent. and Plant Quar. 1953. Report of forest insect surveys in Oregon and Washington. (Oct.) p. 26.
98. Oregon State Board of Forestry and Pac. Northwest Forest and Range Exp. Sta. 1954. Report of forest insect surveys in Oregon and Washington. (Nov.) p. 23.

99. Pacific Northwest Forest and Range Experiment Station. 1952. Annual Report. p. 53.
100. Pacific Northwest Forest and Range Experiment Station. 1955. Annual Report. p. 35.
101. Pacific Northwest Forest and Range Experiment Station. 1956. Annual Report. p. 25.
102. Patterson, J. E. 1930. Control of the mountain pine beetle in lodgepole pine by the use of solar heat. U. S. Dept. Agr. Tech. Bul. 195. 20 pp.
103. Perthunen, V. 1957. Reactions of two bark beetle species, Hylurgops pallintes and Hylastes aster (Col. Scolytidae), to the terpen a-pinene. Annals Entomologici Fennici. 23: 101-10.
104. Peterson, Alvah. 1957. Larvae of insects, introduction to nearctic species. Part II, Coleoptera, Diptera, Neuroptera, Siphonaptera, Mecoptera, Trichoptera. 3rd ed. Edwards Bros., Ann Arbor, Mich. 416 pp.
105. Reid, R. W. 1957. The bark beetle complex associated with lodgepole pine slash in Alberta. Part III. Notes on the biologies of several predators with special reference to Enoclerus sphegeus Fab., and two species of mites. Can. Ent. 89: 111-120.
106. Reid, R. W. 1958. The behavior of the mountain pine beetle, Dendroctonus monticolae Hopk., during mating, egg laying and gallery construction. Can. Ent. 90: 505-509.
107. Reid, R. W. 1958. Internal changes in the female mountain pine beetle, Dendroctonus monticolae Hopk., associated with egg laying and flight. Can. Ent. 90: 464-468.
108. Richmond, H. A. 1935. A morphological study of the bark beetle, Dendroctonus monticolae Hopk. McGill Univ., Faculty of Graduate Studies, unpubl. thesis.
109. Richmond, H. A. and J. M. Kinghorn. 1951. The hemlock looper problem in British Columbia. Forest Chron. 27: 32-37.
110. Richmond, H. A. 1953. Douglas-fir bark beetle in British Columbia. B. C. Lumberman 37(5): 43, 90, 92.

111. Rudinsky, J. A. and J. P. Vite¹. 1956. Effects of temperature upon the activity and behavior of the Douglas fir beetle. *Forest Sci.* 2: 259-267.
112. Rudinsky, J. A. and L. C. Terriere. 1959. Laboratory studies on the relative contact and residual toxicity of ten test insecticides to Dendroctonus pseudotsugae Hopk. *Jour. Econ. Ent.* 52: 485-499.
113. Rudinsky, J. A. 1960. Forest insect survey and control methods. Ore. State College, Corvallis, Ore. 55 pp. *Proc.*
114. Rust, H. J. 1933. Many bark beetles destroyed by predacious mite. *Jour. Econ. Ent.* 26: 733-734.
115. Ryan, Roger. 1959. Termination of diapause in the Douglas-fir beetle, Dendroctonus pseudotsugae Hopkins, as an aid to continuous laboratory rearing. *Can. Ent.* 91: 520-525.
116. Silver, G. T. and D. A. Ross. 1954. Annual report of the forest insect and disease survey. Canada Dept. Agr. Forest Biol. Div. p. 117.
117. Silver, G. T. and D. A. Ross. 1955. Annual report of the forest insect and disease survey. Canada Dept. Agr. Forest Biol. Div. p. 93-94.
118. Silver, G. T. and D. A. Ross. 1956. Annual report of the forest insect and disease survey. Canada Dept. Agr. Forest Biol. Div. p. 81.
119. Silver, G. T. and D. A. Ross. 1957. Annual report of the forest insect and disease survey. Canada Dept. Agr. Forest Biol. Div. p. 75.
120. Silver, G. T. and D. A. Ross. 1958. Annual report of the forest insect and disease survey. Canada Dept. Agr. Forest Biol. Div. p. 87.
121. Smyth, Arthur V. 1959. The Douglas-fir bark beetle epidemic on the Millicoma Forest: Methods used for control and salvage. *Jour. Forestry* 57: 278-280.
122. Struble, G. R. 1942. Biology of two native Coleopterous predators of the mountain pine beetle. *Pan Pacific Ent.* 18: 97-107.

123. Swaine, J. M. 1918. Canadian bark-beetle, Part II. A preliminary classification with an account of the habits and means of control. Canada Dept. Agr. Ent. Branch Bul. 14. 143 pp.
124. Thomas, J. B. 1957. The use of larval anatomy in the study of bark beetles (Coleoptera: Scolytidae). Can. Ent. 89: Supplement 5, 45 pp.
125. Trappe, James M. 1953. Review of the Douglas-fir beetle epidemic in western Oregon and Washington and investigations of reduced tree vigor as a causal factor. Report submitted to the Coll. of Forestry, Univ. of Wash. 18 pp. Typed.
126. U. S. Bureau of Entomology and Plant Quarantine, Forest Insect Laboratory. 1953. An evaluation of forest insect and disease research needs in Oregon and Washington, Part I, Insects. 27 pp. (Advisory to Northwest Forest Pest Action Committee).
127. Vite, J. P. and J. A. Rudinsky. 1957. Contribution toward a study of Douglas-fir beetle development. Forest Sci. 3: 156-167.
128. Walters, H. and K. Graham. 1952. Douglas-fir beetle in the interior of British Columbia. Canada Dept. Agr. Bi-Mo. Progr. Rpt. 8(5): 2.
129. Walters, J. 1953. Investigations of the Douglas-fir beetle, I. Tree classification; II. Flight study of the Douglas-fir beetle. Canada Dept. Agr. Forest Biol. Lab., Vernon, B. C. Ann. Tech. Rpt.
130. Walters, J. 1955. Bionomics of the Douglas-fir beetle, Dendroctonus pseudotsugae Hopk, in the interior of British Columbia. Canada Dept. Agr. Forest Biol. Lab., Vernon, B. C. Interim Rpt. 1954-2. 34 pp.
131. Walters, J. 1955. Douglas-fir beetle associated with winter injury. Canada Dept. Agr. Bi-Mo. Progr. Rpt. 11(4): 4.

132. Walters, J. and D. K. Campbell. 1955. Mites as agents of natural control of the Douglas-fir beetle. Canada Dept. Agr. Bi-Mo. Progr. Rpt. 11(1): 3-4.
133. Walters, J. 1956. Biology and control of the Douglas-fir beetle in the interior of British Columbia. Canada Dept. Agr. Forest Biol. Div. Publ. 975. 11 pp.
134. Warren, G. L. 1958. A method of rearing bark and cambium-feeding beetles with particular reference to Hylobius warreni Wood. Can. Ent. 90: 425-428.
135. Wear, J. F. and J. R. Dilworth. 1955. Color photos aid salvage. Lumberman 82(13): 88.
136. Wear, J. F. and P. G. Lauterbach. 1955. Color photographs useful in evaluating mortality of Douglas-fir. Soc. Amer. Foresters Mtg. Proc. p. 169-171.
137. Werner, A. E. and K. Graham. 1957. Volatile wood constituents in relation to ambrosia beetle. Canada Dept. Agr. Bi-Mo. Progr. Rpt. 13(4): 3.
138. Whiteside, J. M. 1955. Report of forest insect surveys in Oregon and Washington. Pac. Northwest Forest and Range Exp. Sta. p. 27-28.
139. Whiteside, J. M. 1957. Forest insect conditions in the Pacific Northwest during 1956. Pac. Northwest Forest and Range Exp. Sta. p. 15.
140. Whiteside, J. M. 1958. Forest insect conditions in the Pacific Northwest during 1957. Pac. Northwest Forest and Range Exp. Sta. pp. 18-19.
141. Wichmann, H. E. 1953. Rindenbrüter und Hallimasch. Forstwiss Cbl. 72(1/2): 57-63.
142. Wright, Ernest and K. H. Wright, 1954. Deterioration of beetle-killed Douglas-fir timber. Pac. Northwest Forest and Range Exp. Sta. Research Pap. 10, 11 pp.
143. Wright, Kenneth H. 1950. The effect of precipitation and its seasonal distribution on ring-growth of Douglas-fir stands attacked by Dendroctonus pseudotsugae Hopk. in western Oregon. Duke Univ. School of Forestry. Unpubl. thesis. 40 pp.
144. Wright, K. H. 1952. The current Douglas-fir beetle outbreak in western Oregon and southwest Washington. Western Forestry Conf. Ann. Proc. 43: 53-55.

145. Wright, K. H. and L. H. McMullen. 1955. Presentation on Douglas-fir beetle at the 7th Ann. Forest Insect Work Conf., Dec. 1955, Spokane, Wash. In proceedings, unpublished.
146. Wright, K. H. and P. G. Lauterbach. 1958. Ten year study of mortality in a Douglas-fir saw-timber stand in Coos and Douglas Counties, Oregon. Pac. Northwest Forest and Range Exp. Sta. Research Pap. 27. 12 pp.

APPENDIX--OUTLINE FOR STUDY OF BARK BEETLES, ADAPTED FROM SWAINE,
WITH REFERENCES TO "LITERATURE CITED" ON DOUGLAS-FIR BEETLE

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LIFE HISTORY

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